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Usnea subfloridana Stirt. (Parmeliaceae) and Its Related Species in Eastern Asia

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Usnea subfloridana Stirt. and its related species in eastern Asia are taxonomically revised. Five species, *U. florida*, *U. fulvoreagens*, *U. glabrescens*, *U. wasmuthii* as well as *U. subfloridana* are recognized. While *U. florida* forms no asexual propagule, the other four are sorediate. Soralia morphology is particularly useful for distinguishing these four species, since its origin and development are different. Among the five species treated here, *U. fulvoreagens* and *U. wasmuthii* are newly recorded for eastern Asia.

Key words: eastern Asia, lichenized ascomycetes, soralia, taxonomy, *Usnea*

When Asahina (1956, 1959a, 1959b) revised *Usnea* subsect. Comosae (sensu Motyka 1936–38) in eastern Asia, he recognized *U. comosa* (Ach.) Vain., nom. illeg. (= *U. subfloridana* Stirt.) and *U. glabrescens* (Nyl.) Vain. According to him, these two species were separated mainly by the soralia with convex or concave top. He also recognized four subspecies under *U. comosa* based on their chemical characters; subsp. *colorans* Asahina, subsp. *comosa*, subsp. *melanopoda* Asahina and subsp. *praetervisa* Asahina. In addition, he considered *U. glabrescens* to include three subspecies also separated by their chemical characters; subsp. *asiatica* Asahina, subsp. *glabrescens*, and subsp. *pseudocolorans* Asahina. In addition, Asahina (1968) reported *U. florida* (L.) F.H.Wigg. from Taiwan, which is closely related to *U. subfloridana* and *U. glabrescens*.

Asahina (1956, 1959a, 1959b) recognized that the absence or presence of soralia with convex or concave tops are characteristic of the species. However, when Clerc (1987a, 1987b, 1992) studied *U. subfloridana* and its related species, following features of soralia are also recognized as important characters; shape and size, convex or concave tops, presence or absence of isidiomorphs, and the degree of excavating. In addition, Clerc and Herrera-Campos (1997) emphasized the importance of the origin where soralia begin their development.

The aim of the present study is to revise *U. subfloridana* and its related species in eastern Asia, based on the discussion of soralia morphology.

Materials and Methods

The study is primarily based on herbarium specimens housed in the National Science Museum, Tokyo (TNS) as well as the specimens collected by the present authors through field works in 1994–1997. Field trips were made in Japan (Hokkaido,

Honshu, Shikoku, and Kyushu). The total number of specimens used for the study was 133. Although they all are preserved in TNS, only representatives of them are cited in this paper. Type specimens preserved in BM, H, LINN, TNS, and TUR were also studied.

Morphological observation was made using a dissecting microscope. The diameter of branches and the thickness of the cortex, medulla and axis were measured at the well-developed thicker branches under × 50 magnification. The ratio of the thickness of the cortex, the medulla and the axis, can be given following Clerc (1984, 1987a). The anatomical observation was carried out using a bright field microscope. Sections for anatomical studies of apothecia were made by hand-razor. They were observed in GAW solution.

Lichen substances of specimens including type specimens were studied by means of thin layer chromatography (TLC) (Culberson and Johnson 1982) or microchemical crystal tests (Asahina 1956) when necessary. Only the solvent B system (hexane: methyl *tert*.-butyl ether : formic acid = 140:72:18) was employed for TLC tests.

Results and Discussion

Usnea subfloridana Stirt. and its related species are well delineated with the following characters: 1) the fruticose, erect to subpendent thallus with a jet black base; 2) the terete, not inflated, gradually tapering branches with mat surface and usually with numerous lateral branches and fibrils; 3) the presence of verrucose to cylindrical papillae on thicker branches; 4) production of depsides or depsidones (Figs. 1–2, Table 3).

As a result of the present study, five species, *U. florida*, *U. fulvoreagens*, *U. glabrescens*, *U. subfloridana* and *U. wasmuthii* are recognized in the present area. Of the five species of the present group, *U. florida* is the only species forming no soralia and can be readily distinguished from the others. In other four species, soralia morphology is of taxonomic importance as discussed by Clerc (1987b). Although soralia are variable in morphology as mentioned below, they show rather stable features as described under the description of each species and in Table 1. Soralia are elliptic or rounded in the vertical view or confluent each other to form irregular mass of asexual propagules. They have convex or concave tops and slightly to distinctly elevated from the surface of branch which look like being stipitate. Cortical margins of soralia are perpendicular to the surface of branch or are reflexed outside of soralia. Isidiomorphs and/or granular soredia are formed on soralia in certain species. When isidiomorphs are formed, they are very few or abundant.

Soralia of this group are convex or concave at the top when matured, and can be divided into two types; one with convex top (type 1) and another with concave top (type 2). Convexity or concavity at the top of soralia is correlated with the presence or absence of granular soredia. When granular soredia are only produced on soralium, they can be easily separated, resulting the top of soralium to be concave. When isidiomorphs are generated on soralium, the top of soralium becomes convex. The juvenile stage of isidiomorphs sometimes looks like granular soredia, but they can be distinguished by the presence of cortex on the surface of granules.

Soralia of the type 1 are developed from the top of eroded papillae, and those of type 2 are developed directly from cortex. Although four origins of soralia in *Usnea* are reported by Clerc and his co-workers (Clerc 1987a, Clerc and Herrera-Campos 1997, Herrera-Campos et al. 1998), which are 1) the top of eroded papillae, 2) the scars of detatched fibrils, 3) the cracks, and 4) the cortex, the origins from scars of detatched

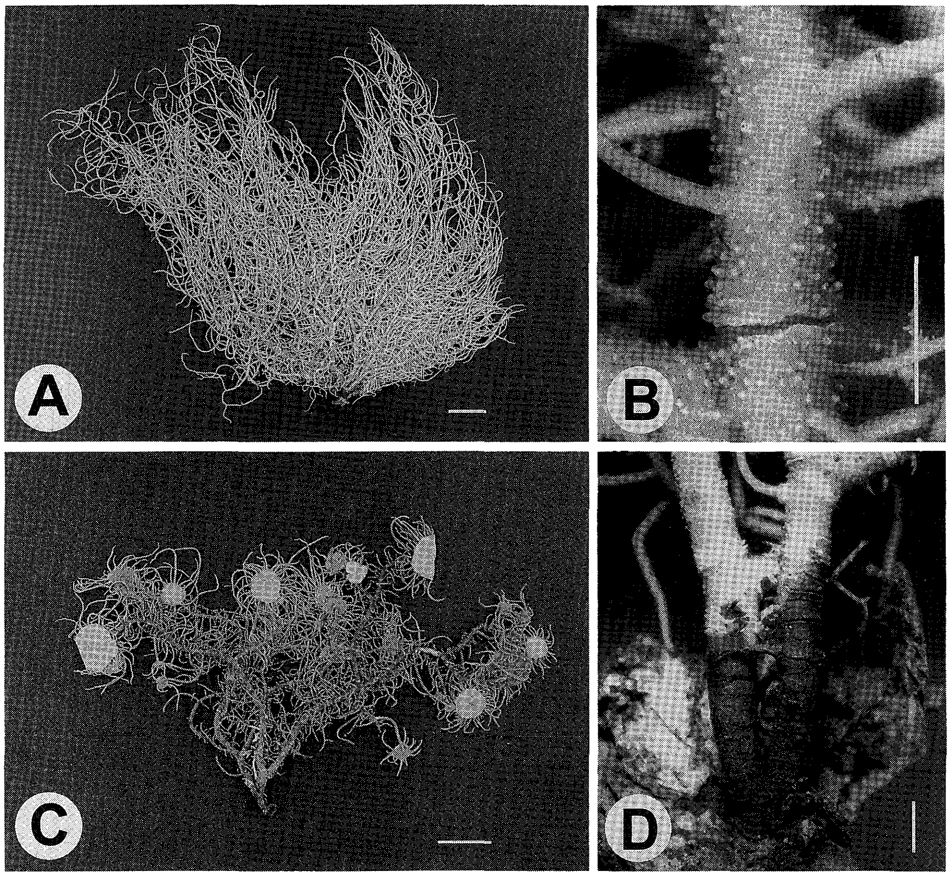

Fig. 1. Diagnostic characters of *Usnea subfloridana* and its related species. A. Sterile thallus of *U. subfloridana.* (Yanagawa, Mt. Yatsugatake. July 25, 1959, M. Togashi and S. Kurokawa s.n.). B. Papillae of *U. subfloridana* on thicker branches. (Y. Ohmura 2900a). C. Fertile thallus of *U. florida.* (collector unknown 106). D. Jet black base of thallus of *U. glabrescens.* (Y. Ohmura 3824b). Scales =1 cm (A and C), and 1 mm (B and D).

fibrils and cracks are not predominantly involved in this group. When soralia are developed from the top of eroded papillae, they are usually stipitate and their cortical margins are not reflexed outside of soralia. When soralia are developed from the top of very early stage of papillae, they look like sessile even if they increase in mass. However, in the case of development from mature stage of papillae, soralia is stipitate even if they enlarge their masses. This type is commonly found in *U. subfloridana.* When soralia are developed directly from cortex, their cortical margins are slightly or distinctly reflexed outside as they grow. This type of soralia may be caused by the pressure of increasing of hyphae and algae under the cortex. This type is predominant in *U. fulvoreagens*, *U. glabrescens* and *U. wasmuthii.* Thus, the soralia morphology is correlated with their origins and ontogeny, and considered to be of taxonomic importance to distinguish the species of this group.

In addition, soralia of *U. fulvoreagens*, *U. subfloridana* and *U. wasmuthii* are confluent

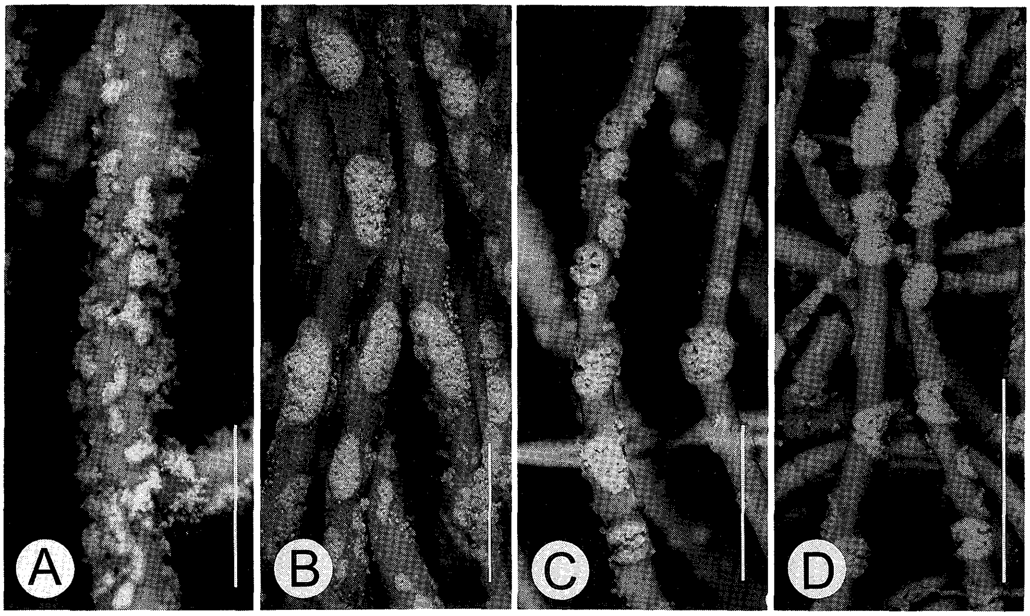

Fig. 2. Soralia of *Usnea subfloridana* and its related species. A. Convex soralia with numerous isidiomorphs (*U. subfloridana*, Y. Ohmura 2900a). B. Concave soralia with slightly excavating surface forming elliptic masses of soredia. (*U. wasmuthii*, T. Matsuoka s.n.). C. Concave soralia with slightly excavating surface forming rounded masses of soredia (*U. glabrescens*, Y. Ohmura 3824b). D. Concave soralia with deeply excavating surface, and the cortical margin distinctly reflexed (*U. fulvoreagens*, H. Kashiwadani 19907). Scales =1 mm.

with adjacent soralia as they grow, while those of *U. glabrescens* are more or less discrete when they contact with an adjacent soralium as reported by Clerc (1992). Although the nature of confluence or discreteness of soralia has not been well studied, this is usually correlated with another feature (e.g., chemistry). Therefore, whether soralia are confluent or discrete can be accepted as one of taxonomic characters.

Papillae are formed on the surface of thicker branches in all treated species. Although three types of papillae, hemispherical, verrucose (or conical) and cylindrical, are known in *Usnea* as reported by Swinscow and Krog (1979) and Clerc (1987a), papillae of *U. subfloridana* and its related species become cylindrical when matured. However, height and amount of papillae vary depending on their developmental stage and/or by environmental conditions. The larger projection, which contains medullary tissue, is called a tubercle by Swinscow and Krog (1979). However, this structure is treated here as a papilla, since presence or absence of medullary tissue in papillae is variable among sorediate species of the genus *Usnea*.

Although the ratio of thickness of the cortex, medulla and axis (CMA) of each species was measured, no notable difference was found among them (Table 2).

The chemistry of each species was examined by means of TLC methods, and the results are shown in Table 3. As in most lichen species with pale yellow thalli, usnic acid is constantly produced in the cortex of all species treated. Atranorin, another

Table 1. Soralia morphology in *Usnea subfloridana* and its related species in eastern Asia

Species	Origin of dominated soralia	Shape and Size	Stipes	Cortical margin	Tops	Granular soredia	Isidiomorphs
U. florida	—	—	—	—	—	—	—
U. fulvoreagens	cortex	confluent, irregular, larger than branch diameter	slightly stipitate	distinctly reflexed	concave, deeply excavating into nearly central axis	present	absent
U. glabrescens	cortex	± discrete, rounded, larger than branch diameter	slightly stipitate	slightly reflexed	concave, slightly excavating and never reached to central axis	present	rarely present
U. subfloridana	papillae	confluent, irregular, smaller than branch diameter	often distinctly stipitate	not reflexed	convex	absent	commonly present
U. wasmuthii	cortex	confluent, elliptic to irregularly rounded, larger than branch diameter	slightly stipitate	slightly reflexed	concave, slightly excavating and never reached to central axis	present	occasionally present

Table 2. The ratio of thickness of the cortex, medulla and axis (CMA) in *Usnea subfloridana* and its related species. Mean (italic numeral), standard deviation (no ornament numeral) and extreme values (in the parenthesis) are shown, n=total number of samples examined

Species	Cortex (% of radius)	Medulla (% of radius)	Axis (% of diameter)	Diameter of branch (mm)	n
U. florida	(8.9)–*11*–(13)	(13)–*16*–(17)	(42)–*46*–(48)	(1.1)–*1.2*–(1.3)	3
U. fulvoreagens	(7.4)–9.2–*10*–12–(13)	(14)–18–*22*–26–(28)	(24)–28–*36*–44–(51)	(0.7)–0.9–*1.1*–1.3–(1.4)	11
U. glabrescens	(8.7)–*11*–(14)	(18)–*21*–(25)	(31)–*37*–(46)	(1.0)–*1.2*–(1.3)	3
U. subfloridana	(7.3)–9–*11*–13–(16)	(9.1)–14–*18*–22–(27)	(27)–34–*41*–48–(58)	(0.5)–0.8–*1.0*–1.2–(1.6)	80
U. wasmuthii	(6.5)–8.7–*11*–13–(17)	(7.3)–14–*18*–22–(29)	(29)–37–*43*–49–(57)	(0.7)–0.8–*1.0*–1.2–(1.8)	42

common cortical substance in lichens, is demonstrated in some specimens of *U. fulvoreagens*, though it is a very rare substance in the genus *Usnea*. It should be noted that atranorin is produced in some species of *Ramalina* (Stevens 1987), in which usnic acid is a constant cortical substance, and is considered to be accessory. As regard to depsides, following three biosynthetically different groups are considered: 1) diffractaic acid and its related substances group, 2) barbatic and 4-*O*-demethylbarbatic acids group, and 3) squamatic and/or thamnolic acids group. In the case of presence of diffractaic acid, it always follows barbatic, 4-*O*-demethylbarbatic, baeomycesic, and squamatic acids. According to Yoshimura and Kurokawa (1980) and Yoshimura et al. (1992), the *O*-methyl of diffractaic acid is partially substituted by H_2O to form barbatic acid (= 2-*O*-demethyldiffractaic acid). Similarly, the *O*-methyl of barbatic acid may be substituted by H_2O to form 4-*O*-demethylbarbatic acid. In addition, oxidation of the methyl radical of barbatic acid forms baeomycesic acid, and further oxidation of its radical of baeomycesic acid form squamatic acid. Therefore, these substances are closely related to each other biosynthetically as well as chemically. The presence or absence of one or a few of them can be considered to have certain taxonomic value, even though the concentration of each substance is variable as mentioned in the description of *U. fulvoreagens* in the present study. The biosynthetic and/or chemical relationship between squamatic and thamnolic acids have not been studied extensively so far. However, they are considered as biosynthetically closely related substances as discussed by Culberson (1969), and they often replaces each other in paired races in lichens (Fiscus 1972). Norstictic and salazinic acids belong to depsidone. The chemical difference between them is only presence or absence of a hydroxyl radical. Therefore, they are very closely related substance each other chemically. The occurrence of zeorin in *U. fulvoreagens* is particularly interesting from a chemotaxonomic viewpoint. Zeorin is synthesized through the mevalonic acid pathway, while depsides and depsidones are produced through the acetyl-polymalonyl pathway. Thus, the presence of zeorin can be considered to have rather important taxonomic value, especially in separating species.

Although *U. fulvoreagens*, *U. subfloridana* and *U. wasmuthii* produce several chemical races as shown in Table 3, no morphological or ecological difference was recognized among them, and it is considered that each chemical race has no necessity to be given any taxonomic ranks.

Taxonomic treatment

Usnea florida (L.) Weber ex F.H.Wigg., Primit. Flor. Holsat. 91 (1780).

Lichen floridus L., Spec. Pl. **1**: 1156 (1753). Lectotype (selected by Clerc 1984): Sweden?, Linne? (LINN !). Chemistry: alectorialic (in apothecia), bourgeanic, hypothamnolic, thamnolic and usnic acids (by Jørgensen et al. 1994).

Thallus fruticose, erect, up to 6.5 cm long, jet black at the base; branching anisotomic-dichotomous; branches mat on the surface, lacking pseudocyphella, terete, not inflated, gradually tapering, with numerous fibrils and lateral branches, 1.1–1.3 mm in diameter; lateral branches not constricted at the base; papillae common on thicker branches, cylindrical; soralia absent. Cortex moderate in thickness, 8.9–13% of the radius. Medulla dense, moderate in thickness, 13–17% of the radius. Axis solid, moderate in thickness, 42–48% of the diameter. Apothecia common, subterminal on terminal and lateral branches, up to 6.5 mm in diameter, flat; disc pruinose; epihymenium 4–15 μm high;

Table 3. Lichen substances in *Usnea subfloridana* and its related species. +, present. −, absent. tr, trace. ±, accessory substance. Atr, atranorin; Usn, usnic acid; Bar, barbatic acid; Dif, diffractaic acid; 4OB, 4-*O*-demethylbarbatic acid; Bae, baeomycesic acid; Squ, squamatic acid; Tha, thamnolic acid; Nor, norstictic acid; Sal, salazinic acid; Zeo, zeorin

Species	Race	Cortical substance		Medullary substance								
				Depside						Depsidone		Terpenoid
		Atr	Usn	Bar	Dif	4OB	Bae	Squ	Tha	Nor	Sal	Zeo
U. florida		−	+	−	−	−	−	−	+	−	−	−
U. fulvoreagens	Race 1	−	+	−	−	−	−	−	−	+	−	+
	Race 2	±	+	tr	+	tr	tr	tr	−	+	−	+
U. glabrescens		−	+	−	−	−	−	−	−	+	+	−
U. subfloridana	Race 1	−	+	−	−	−	−	−	+	−	−	−
	Race 2	−	+	−	−	−	−	+	−	−	−	−
	Race 3	−	+	−	−	−	−	+	+	−	−	−
	Race 4	−	+	−	−	−	−	−	−	+	−	−
U. wasmuthii	Race 1	−	+	−	−	−	−	−	−	−	+	−
	Race 2	−	+	+	−	+	−	−	−	−	+	−
	Race 3	−	+	−	−	−	−	−	+	−	−	−

hymenium 56–70 μm high; hypothecium 30–60 μm high; spores 8–10 × 4–6 μm.

Chemistry: usnic and thamnolic acids.

From the lectotype of the present species, Jørgensen et al. (1994) reported the occurrence of alectorialic (in apothecia), bourgeanic and hypothamnolic acids as well as usnic and thamnolic acids. The former three substances can be considered accessory as pointed out by Clerc (1984). A specimen collected in Taiwan well agrees with the type and coincides very well with the description given by Clerc (1984).

Usnea florida is frequently confused with *U. masudana* Asahina, *U. ogatai* Asahina, *U. orientalis* Motyka, *U. pseudogatai* Asahina, *U. shimadai* Asahina and *U. sinensis* Motyka, since they all occur in Japan and/or Taiwan and form similar thalli lacking soralium with numerous apothecia. However, *U. florida* is easily distinguished from the other six species by the jet black base of thallus and by the production of thamnolic acid.

Asahina (1968) reported the occurrence of *U. florida* from Taiwan. This is the only record for the species in the present area, though it is widely distributed in Europe (Clerc 1984).

Specimen examined. Taiwan, Prov. Taitung, Mt. Dai-wu, on bark, elevation about 2000 m, September, 1958, collector unknown 106.

Usnea fulvoreagens (Räsänen) Räsänen, Lich. Fenn. Exs. 13 (1935).

Usnea glabrescens (Nyl.) Vain. var. *fulvoreagens* Räsänen, Flecht. Estlands I, **34:** 20 (1931). Holotype: Russia, Karelian Republic, Kl. Kurkijoki, Lapinlahti, August 22, 1923, Räsänen s.n. (H !). Chemistry: usnic, norstictic, menegazziaic, stictic, constictic acids, and zeorin (trace).

Thallus fruticose, erect to subpendent, up to 16 cm long, jet black at the base; branching isotomic- or anisotomic-dichotomous; branches mat on the surface, lacking pseudocyphella, terete, not inflated, gradually tapering, with numerous fibrils and lateral branches, 0.7–1.4 mm in diameter; lateral branches not constricted at the base; papillae common to sparse on thicker branches, cylindrical to verrucose; soralia

common, formed mainly on terminal and lateral branches, developed from cortex, concave at the top, deeply excavating often into nearly central axis, without isidiomorphs, sessile or often slightly stipitate, often confluenting each other to form irregular masses of soredia larger than the branch diameter, cortical margin distinctly reflexed; soredia granular. Cortex moderate in thickness, 7.4–13% of the radius. Medulla moderate to dense, 14–28 % of the radius. Axis solid, moderate in thickness, 24–51% of the diameter. Apothecia not seen.

Chemistry: Race 1, usnic, norstictic acids, and zeorin; Race 2, usnic, norstictic, diffractaic acids and zeorin, and trace amount of barbatic, 4-*O*-demethylbarbatic, baeomycesic, squamatic acids, and atranorin (±).

Usnea fulvoreagens is distinguished from other related species by having deeply excavating soralia without isidiomorph, and by the presence of norstictic acid and zeorin.

Two chemical races were recognized within *U. fulvoreagens* from the present area as shown above. No morphological or ecological difference was found between Race 1 and Race 2. Therefore, it is considered that the chemical differences of this species have no taxonomic value. Although diffractaic acid is always present in the thalli of Race 2, its concentration is not uniform even within a thallus. When two or three different parts of the thallus were examined, the concentration of the acid is apparently variable, being detected as a distinct or a pale ambiguous spot on TLC plate.

Although menegazziaic, stictic and constictic acids were detected in the holotype specimen of *U. fulvoreagens* , they were not detected in specimens in the investigated area. However, no morphological difference was observed between the type and other specimens. It is noted that Race 1 and Race 2 of *U. fulvoreagens* in the present paper are also known from Europe and North America (Clerc 1992, Halonen et al. 1998, Purvis et al. 1992).

In Japan, *U. fulvoreagens* is distributed in Hokkaido to central Honshu, where it grows on tree barks such as *Abies*, *Larix* and *Salix*. It is found at elevations between 50 and 1800 m (at lower elevation in Hokkaido and at higher elevations in central Honshu). In Taiwan, it grows on barks at elevations between 1500 and 2600 m. Although *U. fulvoreagens* has been reported from Europe and North America (Clerc 1992, Halonen et al. 1998, Purvis et al. 1992), this is the first record from eastern Asia.

Representative specimens examined. Race 1. JAPAN. Hokkaido. Prov. Nemuro: Ochiishi, on bark of *Abies sachalinensis*, elevation about 50 m, September 1, 1965, S. Kurokawa 65808. Honshu. Prov. Kai: Tokusa Pass, August 7, 1953, S. Kurokawa 521244. Prov. Shinano: en route from Azusayama to Jumonji Pass, Kawakami-mura, Minamisaku-gun, elevation about 1600 m, June 13, 1983, H. Kashiwadani 19907. TAIWAN. En route from Ssu-yuan to To-chia-tun Shanm Mt. Nanhuta Shan, Hoping, on bark of Salix sp., elevation 1900–2250 m, November 9, 1989, H. Kashiwadani 35767.

Race 2. JAPAN. Honshu. Prov. Shinano: ca. 3 km ESE of Azusayama, Kawakami-mura, Minamisaku-gun, on bark of *Larix kaempferi*, elevation 1460–1500 m, December 9, 1996, Y. Ohmura 2906. TAIWAN. Mt. Nan-Fu-Ta-San, elevation 1500–2400 m, January 19, 1964, S. Kurokawa 963.

Usnea glabrescens (Nyl.) Vain., Meddel. Soc. Fa. Fl. Fenn. **48**: 173 (1925).

Usnea barbata (L.) F. H. Wigg. var. *glabrescens* Nyl. in Vainio Meddel. Soc. Fa. Fl. Fenn. **2**: 46 (1878). Holotype: Finland, Tavastia australis, Korpilahti, Tianea, 1873, E. Lang s.n. (TUR !). Chemistry: usnic, norstictic, protocetraric (trace), salazinic acids, and atranorin.

Thallus fruticose, erect to subpendent, up to 16 cm long, jet black at the base; branching isotomic-dichotomous; branches mat on the surface, lacking pseudocyphella,

terete, not inflated, gradually tapering, with sparse fibrils and lateral branches, 1.0–1.3 mm in diameter; lateral branches not constricted at the base; papillae common on thicker branches, verrucose; soralia common, formed mainly on terminal and lateral branches, developed from cortex, concave at the top, slightly excavating, rarely with isidiomorphs, sessile or often slightly stipitate, more or less discrete, rounded in shape, sometimes becoming larger than branch diameter, cortical margin usually slightly reflexed; soredia granular. Cortex moderate in thickness, 8.7–14% of the radius. Medulla moderate to dense, moderate in thickness, 18–25% of the radius. Axis solid, moderate in thickness, 31–46% of the diameter. Apothecia not seen.

Chemistry: usnic, norstictic and salazinic acids.

Although atranorin and a trace amount of protocetraric acid were detected in the holotype specimen of *U. glabrescens*, they were not detected in specimens in the investigated area. However, no morphological difference was observed between the type and other specimens. The presence or absence of them seems to have no taxonomic value.

Asahina (1959a, 1959b) reported three subspecies under *U. glabrescens* which were separated by the chemistry: 1) subsp. *glabrescens* characterized by norstictic acid, 2) subsp. *asiatica* Asahina by salazinic acid, and 3) subsp. *pseudocolorans* Asahina by thamnolic acid. In the present paper, however, subsp. *asiatica* and subsp. *pseudocolorans* are treated as synonyms of *U. wasmuthii* (see note under *U. wasmuthii*).

Usnea glabrescens resembles *U. fulvoreagens* in having concave soralia and in producing norstictic acid. However, it can be distinguished from *U. fulvoreagens* by the discrete soralia with slightly excavating surface. It also differs in the absence of zeorin which is constantly produced in *U. fulvoreagens*.

In Japan, *U. glabrescens* is found in central Honshu, where it grows on tree bark (e.g., *Salix*) at elevations between 1440 and 1800 m. In Taiwan, this species grows on twigs (e.g., *Osmanthus*) at elevations between 2400 and 2600 m. *Usnea glabrescens* is widely distributed in boreal to temperate regions in Europe, eastern Asia and North America (Asahina 1959a, Halonen et al. 1998, Purvis et al. 1992).

Specimens examined. **JAPAN**. Honshu. Prov. Shinano: en route from Gyozya-goya to Minoto-sanso, Yatsugatake Mts., Chino-city, on bark of *Salix* sp., elevation 1740–1800 m, August 29, 1997, Y. Ohmura 3824b. **TAIWAN**. Mt. Nan-Fu-Ta-San, on twigs of *Osmanthus bioritsuensis*, elevation 2400–2600 m, January 20, 1964, S. Kurokawa 1088.

Usnea subfloridana Stirt., Scot. Natur. **6**: 294 (1882).

Holotype: Scotland, Perthshire, Killin, July 19, 1881, Stirton s.n. (BM !). Chemistry: usnic and thamnolic acids.

Lichen comosus Ach., Kgl. Vetensk. Acad. Nya Handling. 209, tab. 8, fig. 1 (1795) – *Usnea plicata* (L.) F.H.Wigg. var. *comosa* (Ach.) Ach., Method. Lich. 311 (1803); Röhl., Deutsch. Fl. **3**(2): 144 (1813) – *U. florida* var. *comosa* (Ach.) Biroli, Flora Asconiens. **2**: 199 (1808) – *U. comosa* (Ach.) Vain., in Norrl. and Nyl., Herb. Lich. Fenn. exs. No. 457, 458 (1921); Motyka, Lich. Gen. *Usnea* Stud. Monogr., pars. syst., 264 (1936); non *U. comosa* Pers. (1826). Holotype: Sweden, Acharius? (H !). Chemistry: usnic, thamnolic and hypothamnolic acids (annotated by Clerc).

Usnea comosa subsp. *colorans* Asahina, Lich. Jap. **3**: 94, 1956, syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Kai, Yoshida-guchi 1-gome, Mt. Fuji, August 10, 1952, M. Togashi s.n., pr. maj. p. (TNS !). Chemistry: usnic and thamnolic acids.

Usnea comosa subsp. *praetervisa* Asahina, Lich. Jap. **3**: 95, 1956, syn. nov. Lectotype (selected here): Japan, Honshu,

Prov. Kai, Asahigaoka, Lakeside of Yamanaka, Nakano-mura, Minami-Tsuru-gun, July 30, 1954, S. Kurokawa 540328 (TNS !). Chemistry: usnic and norstictic acids.

Thallus fruticose, erect to subpendent, up to 13.5 cm long, jet black at the base; branching anisotomic- or isotomic-dichotomous; branches mat on the surface, lacking pseudocyphella, terete, not inflated, gradually tapering, usually with numerous fibrils and lateral branches, 0.5–1.6 mm in diameter; lateral branches not constricted at the base; papillae common on thicker branches, verrucose to cylindrical; soralia common, formed mainly on terminal and lateral branches, developed from the top of eroded papillae, convex at the top, usually with numerous isidiomorphs, sessile or often distinctly stipitate, sometimes confluenting each other forming irregular masses of soredia, usually smaller than branch diameter, cortical margin not reflexed; soredia farinose. Cortex moderate in thickness, 7.3–16% of the radius. Medulla moderate to dense, 9.1–27% of the radius. Axis solid, moderate in thickness, 27–58% of the diameter. Apothecia very rare, lateral on terminal and lateral branches, up to 3.0 mm in diameter, cup-shaped; disc pruinose; epihymenium 6–18 μm high; hymenium 60–80 μm high; hypothecium 60–90 μm high; spores 8–10 $\times$ 4–6 μm.

Chemistry: Race 1, usnic and thamnolic acids; Race 2, usnic and squamatic acids; Race 3, usnic, thamnolic and squamatic acids; Race 4, usnic and norstictic acid.

Although this species has been well known as *U. comosa* (Ach.) Vain. (1921) by Japanese lichenologists, the name is illegitimate because it is a later homonym of *U. comosa* Pers. (1826) [ICBN 53.1 (Greuter et al. 1994)]. It is replaced by the name *U. subfloridana* Stirt. which has priority [ICBN 58.1 (Greuter et al. 1994)] (Laundon 1965).

The type specimen of *U. comosa* subsp. *colorans* includes 95 individuals in a packet. Seventy-nine of 95 contain thamnolic acid. The thalli containing thamnolic acid well coincide with the protologue given by Asahina (1956). The rest is a mixture of *U. subfloridana* containing squamatic acid, *U. hakonensis*, *U. pangiana* and *U. wasmuthii*. Specimens containing thamnolic acid were designated here as the lectotype of *U. comosa* subsp. *colorans*, which is well identical with the type specimen of *U. subfloridana*.

When Asahina (1956) described *U. comosa* subsp. *praetervisa*, he cited three specimens: two specimens collected in Japan (Nakasaroma, Kitami, Hokkaido; and Asahigaoka, Yamanaka, Mt. Fuji) and one in China (Kanto, Kinso, Konshun). However, the specimen collected from Nakasaroma was not located in TNS. Specimens collected from Asahigaoka and China agree well with the protologue given by Asahina (1956). The collection from Asahigaoka (S. Kurokawa 540328, July 30, 1954) which is marked as "Typus" on the herbarium packet by Asahina is selected here as the lectotype. The lectotype of *U. comosa* subsp. *praetervisa* is well identical with Race 4 of *U. subfloridana*.

Therefore, *U. comosa* subsp. *colorans* and subsp. *praetervisa* are reduced to synonyms of *U. subfloridana* in the present paper.

Asahina (1956) described one more subspecies, subsp. *melanopoda*, under *U. comosa*. For subsp. *melanopoda*, see note under *U. wasmuthii*.

Usnea subfloridana is easily distinguished morphologically from the related species by having convex soralia. Four chemical races were recognized in *U. subfloridana* from the present area as shown above. The most common race was the Race 1 (thamnolic acid containing race, 74%). Race 2 (squamatic acid containing race, 16%) and Race 4 (norstictic acid containing race, 9%)

were occasionally found. Only one specimen of Race 3 (both thamnolic and squamatic acid containing race, 1%) was found. No morphological or ecological difference was found among the four chemical races. Races 1–3 are very closely related in the chemistry. Therefore, Races 1–3 can be considered to belong to a single species. Even though Race 4 produces norstictic acid, a depsidone, a biosynthetically distant compound from depsides produced in Races 1–3, no notable difference is found among three races. Thus, Race 4 is tentatively treated here as a chemical race of *U. subfloridana* in the present paper, and final taxonomic decision should be made when more materials will be studied.

In Japan, *U. subfloridana* is distributed from Hokkaido to central Honshu, where it grows on twigs or barks of coniferous trees such as *Larix* and *Tsuga*, or deciduous trees such as *Acer*, *Betula*, and *Prunus*. It is found at elevations between 50 and 2000 m (at lower elevations in Hokkaido and at higher elevations in central Honshu). In Taiwan, it grows on bark at high elevations between 2400 and 3300 m. This species is also collected from China and Korea. *Usnea subfloridana* is widely distributed in northern boreal to temperate regions in Europe, Asia and North America (Asahina 1956, Awasthi 1986, Halonen et al. 1998, Motyka 1936–38).

Representative specimens examined.

Race 1. **JAPAN**. Honshu. Prov. Musashi: Mt. Mitsumine, Chichibu, August 30, 1951, S. Kurokawa 510069. Prov. Shinano: Ikenodaira, Takato-cho, Kamiina-gun, on bark of *Larix kaempferi*, elevation 1620 m, June 29, 1997, Y. Ohmura 3144b; Yanagawa, Mt. Yatsugatake, July 25, 1959, M. Togashi and S. Kurokawa s.n. Prov. Kai: Yoshida-guchi 1-gome, Mt. Fuji, August 10, 1952, M. Togashi s.n. TAIWAN. Mt. Chien-San, Mt. Shin-Kao-San, elevation 3100–3300 m, January 1, 1964, S. Kurokawa 279. KOREA. Kanko, 1934, H. To s.n.

Race 2. **JAPAN**. Hokkaido. Prov. Kitami: Nakasaroma. July 2, 1953, M. Tatewaki s.n. Honshu. Prov. Shimotsuke: W Lakeside of Yunoko, Nikko, on bark of *Prunus ssiori*, elevation about 1480 m, July 16, 1995, Y. Ohmura 1122. Prov. Shinano: ca. 3 km ESE of Azusayama, Kawakami-mura, Minamisaku-gun, on bark of *Larix kaempferi*, elevation 1460–1500 m, December 9, 1996, Y. Ohmura 2900a. Prov. Kai: Yoshida-guchi 1-gome, Mt. Fuji, August 10, 1952, M. Togashi s.n. CHINA. Kanto, Kinso, Konshun, May 16, 1943, S. Asahina (herb. Y. Asahina 43516).

Race 3. **JAPAN**. Honshu. Prov. Shinano: en route from Azusayama to Jyumonji Pass, Minamisaku-gun, on bark of *Tsuga diversifolia*, elevation 1860–2030 m, December 9, 1996, Y. Ohmura 2863b.

Race 4. **JAPAN**. Hokkaido. Prov. Tokachi: Shimonozuka, July 3, 1953, Y. Asahina and M. Togashi s.n. Honshu. Prov. Shinano: Shinyu Hot Spring, Mt. Tateshina, May 21, 1959, Y. Asahina [59524], S. Kurokawa and M. Nuno. TAIWAN. Mt. Chien-San, Mt. Shin-Kao-San, elevation 3100–3300 m, January 1, 1964, S. Kurokawa 287. CHINA. Kanto, Kinso, Konshun, May 16, 1943, S. Asahina s.n.

Usnea wasmuthii Räsänen, Flecht. Estlands I, **34**: 19 (1931).

Holotype: Esthonia, Tallinna, Kakumäe, *Picea*, 1908, Wasmuth s.n. (H !). Chemistry: usnic and barbatic acids (by Clerc 1992).

Usnea comosa subsp. *melanopoda* Asahina, Lich. Jap. **3**: 94 (1956), syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Kai, Yoshida-guchi 1-gome, Mt. Fuji, August 10, 1952, M. Togashi s.n. (Herb. Y. Asahina 52810 pr. min. p., TNS !). Chemistry: usnic and salazinic acids.

Usnea glabrescens subsp. *asiatica* Asahina in J. Jpn. Bot. **34**: 229 (1959), syn. nov. Lectotype (selected here): Japan, Honshu, Prov. Shinano, Shin-yu Hot Spring, Mt. Tateshina, May 21, 1959, Y. Asahina [59530], S. Kurokawa and M. Nuno (TNS !). Chemistry: usnic, barbatic, 4-*O*-demethylbarbatic and salazinic acids.

Usnea glabrescens subsp. *pseudocolorans* Asahina in J. Jpn. Bot. **34**: 292 (1959), syn. nov. Holotype: Japan, Honshu, Prov. Shinano, en route from Yanagawa to Kitazawa, Mt. Yatsuga-dake, July 25, 1959, M. Togashi and S. Kurokawa s.n. (Herb. Y. Asahina 59725, TNS !). Chemistry: usnic

and thamnolic acids.

Thallus fruticose, erect to subpendent, up to 24 cm long, jet black at the base; branching isotomic- or anisotomic-dichotomous; branches mat on the surface, lacking pseudocyphella, terete rarely slightly inflated, gradually tapering, with sparse to dense fibrils and lateral branches, 0.7–1.8 mm in diameter; lateral branches not constricted at the base; papillae irregularly distributed on thicker branches, verrucose to cylindrical; soralia common, formed mainly on terminal and lateral branches, developed from cortex, concave at the top, slightly excavating, usually with isidiomorphs, sessile or often slightly stipitate, sometimes confluenting each other forming elliptic to irregularly rounded masses of soredia, sometimes becoming larger than branch diameter, cortical margin sometimes slightly reflexed; soredia granular. Cortex moderate in thickness, 6.5–17% of the radius. Medulla moderate to dense, thin to moderate in thickness, 7.3–29% of the radius. Axis solid, moderate in thickness, 29–57% of the diameter. Apothecia very rare, lateral on terminal and lateral branches, up to 4.8 mm in diameter, cup-shaped; disc pruinose; epihymenium 4–12 μm high; hymenium 48–64 μm high; hypothecium 30–50 μm high; spores 10–12×6–7 μm.

Chemistry: Race 1, usnic and salazinic acids; Race 2, usnic, barbatic, 4-*O*-demethylbarbatic and salazinic acids; Race 3, usnic and thamnolic acids.

The type specimen of *U. comosa* subsp. *melanopoda* includes 25 individuals. Eight of 25 contain salazinic acid as indicated in the protologue of Asahina (1956). They coincide very well with the morphological features shown in the protologue. The results of TLC tests show that barbatic and 4-*O*-demethylbarbatic acids are also contained in four of eight individuals. The occurrence of these two substances was not mentioned by Asahina (1956). In the present paper, therefore, four individuals containing only salazinic acid along with usnic acid are designated as the lectotype of subsp. *melanopoda*, especially for avoiding further confusion in the typification of the subspecies. It is noted here, the rest (17 individuals) is a mixture of *U. pangiana* Stirt. and *U. subfloridana*.

When Asahina (1959a) described *U. glabrescens* subsp. *asiatica*, he cited two specimens collected in Japan (Ikenotaira, Daimon Pass and Shin-yu Hot Spring in Prov. Shinano). Both specimens agree with the protologue given by Asahina (1959a). A note of the ratio of the cortex, medulla and axis accompanied with the latter specimen agree with the values shown by Asahina (1959a). Thus, the specimen collected at Shin-yu Hot Spring is selected here as the lectotype. The lectotype of *U. glabrescens* subsp. *asiatica* is well identical with Race 2 of *U. wasmuthii*.

In the holotype specimen of *U. glabrescens* subsp. *pseudocolorans*, usnic and thamnolic acids were demonstrated. The subspecies is identical with Race 3 of *U. wasmuthii* morphologically as well as chemically.

As a result, *U. comosa* subsp. *melanopoda*, *U. glabrescens* subsp. *asiatica* and subsp. *pseudocolorans* are reduced to synonyms of *U. wasmuthii* in the present paper.

Usnea wasmuthii resembles *U. subfloridana*, from which it can be distinguished by the concave soralia. It also resembles *U. fulvoreagens* and *U. glabrescens*, because they all have concave soralia. However, it can be distinguished from *U. fulvoreagens* by having isidiomorphs and lacking norstictic acid, and from *U. glabrescens* by the confluenting soralia and lacking norstictic acid.

Three chemical races were recognized within *U. wasmuthii* collected in the present area as shown above. Race 1 (45%) and

Race 2 (50%) were commonly found, but Race 3 is rather rare (5%). Race 3 contains thamnolic acid, a depside, which is biosynthetically distantly related to depsidone such as salazinic acid. However, it is treated as one of chemical races of *U. wasmuthii* in the present paper, since no morphological difference has been found between Races 1–2 and Race 3. It should be noted that Race 3 has been also known from Europe (Clerc 1992).

In Japan, *U. wasmuthii* is distributed in Hokkaido to central Honshu, where it grows on twigs or barks of coniferous trees such as *Abies*, *Larix*, *Picea* and *Tsuga*, or deciduous trees such as *Betula* and *Salix*. It is found at elevations between 330 and 2030 m (at lower elevation in Hokkaido and higher elevations in central Honshu). In Taiwan, it grows on twigs or barks of trees such as *Osmanthus* at elevations between 1500 and 3300 m. This species is also collected from China and Korea. Although *U. wasmuthii* is widely distributed in Europe (Clerc 1992), this is the first record of the species from eastern Asia.

Representative specimens examined.

Race 1. **JAPAN**. Hokkaido. Prov. Tokachi: Shimonozuka, July 3, 1953, Y. Asahina s.n. Honshu. Prov. Shinano: en route from Azusayama to Jyumonji Pass, Minamisaku-gun, on bark of *Tsuga diversifolia*, elevation 1860–2030 m, December 9, 1996, Y. Ohmura 2863a. Prov. Kai: Mt. Mizugaki, August 5, 1953, S. Kurokawa 521148. **TAIWAN**. Mt. Nan-Fu-Ta-San, elevation 1500–2400 m, January 19, 1964, S. Kurokawa 962. CHINA. Prov. Koanhoku, east of Yakesi, May 29, 1949, Y. Asahina s.n.

Race 2. **JAPAN**. Hokkaido. Prov. Kitami: Tokusyoppe, Furuume, Bihoro-cho, Abashirigun, on twigs of *Abies sachalinensis*, elevation about 330 m, July 26, 1997, Y. Ohmura 3602b pr. p. Honshu. Prov. Shinano: Daimon Pass, May 22, 1959, Y. Asahina, S. Kurokawa and M. Nuno s.n.; Izumino-mura, Chino-machi, Suwa-gun, October 15, 1957, T. Matsuoka s.n. **TAIWAN**. Mt. Chien-San, Mt. Shin-Kao-San, elevation 3100–3300 m, January 1, 1964, S. Kurokawa 286. **KOREA**. Kankyo-Nando: Kanchiin, August 2, 1934, F. Fujikawa s.n. **CHINA**. Kanto, Kinso, Konshun, May 16, 1943, S. Asahina s.n.

Race 3. **JAPAN**. Honshu. Prov. Shinano: ca. 3 km ESE of Azusayama, Kawakami-mura, Minamisaku-gun, on bark of *Larix kaempferi*, elevation 1460–1500 m, December 9, 1996, Y. Ohmura 2900b.

Key to *Usnea subfloridana* and its related species in eastern Asia

1. Soralia absent; usually well fertile ················*U. florida* (L.) F.H.Wigg.
1. Soralia present; usually sterile ········· 2
2. Soralia convex at the top ······················*U. subfloridana* Stirt.
2. Soralia concave at the top ············ 3
3. Isidiomorphs absent; soralia often deeply excavating into nearly the central axis; zeorin present ······*U. fulvoreagens* (Räsänen) Räsänen
3. Isidiomorphs present at least in juvenile stages of soralia; soralia slightly excavating and never reached to central axis; zeorin absent ····························· 4
4. Soralia confluent to form elliptic masses of soredia; norstictic acid absent ·······················*U. wasmuthii* Räsänen
4. Soralia discrete, rounded in shape; norstictic acid present ··············*U. glabrescens* (Nyl.) Vain.

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大村嘉人[a]，柏谷博之[b]：**東アジア産ヒゲサルオガセ（ウメノキゴケ科）とその近縁種**

東アジアから報告されている *Usnea comosa*（= *U. subfloridana*），*U. florida*，*U. glabrescens* について分類学的再検討を行った．その結果，*U. florida*（オニハナサルオガセ　新称），*U. fulvoreagens*（クズレヒゲサルオガセ　新称），*U. glabrescens*（オニヒゲサルオガセ　新称），*U. subfloridana*（ヒゲサルオガセ），*U. wasmuthii*（ニセヒゲサルオガセ　新称）の 5 種が東アジアに産することを認めた．これらの種は主にソラリアの有無やソラリアの形，ソラリア頂点の凹凸，顆粒状粉芽や裂芽状粉芽の有無，特定地衣成分の有無などによって特徴づけられる．ソラリアの形態は発生起源や発生様式の違いと関連が認められるため，分類形質の一つとして重視した．なお，報告した種のうち *U. fulvoreagens* と *U. wasmuthii* は東アジア新産である．

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